A NEW CONIFEROUS MALE CONE FROM THE ENGLISH WEALDEN AND A DISCUSSION OF POLLINATION IN THE CHEIROLEPIDIAECAE

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ABSTRACT. The cheirolepidiaceous pollen-bearing cone *Classostrobus comptonensis* is redescribed on the basis of new material from the type locality. A different pollen-bearing cone from the same deposit is described as a new species of *Masculostrobus*. The numerous specimens display a range of variation which probably represents various degrees of maturity. The structure of this new species, which is typically coniferous, is closer to that found in Taxodiaceae or Araucariaceae than any other extant family. It cannot yet be attributed to any leafy shoot.

THE genus *Classostrobus* Alvin *et al.* (1978) was erected for *Classopollis*-containing cones which could not be attributed with certainty to any species of leafy shoot. The type species, *C. comptonensis* Alvin *et al.* (1978) was based on specimens from a plant debris bed of Barremian age exposed at the cliff foot and in the foreshore between Compton Grange Chine (sometimes called Shippard's Chine) and Hanover Point (sometimes called Brook Point) in the Isle of Wight (OS Grid Ref. SZ 377840). The bed contains abundant shoot fragments and wood of the cheirolepidiaceous conifer, *Pseudofrenelopsis parceramosa* (Fontaine) Watson (Watson 1977; Alvin *et al.* 1981; Alvin 1983). *Classostrobus comptonensis* was attributed to this plant on the basis of association, and on cuticle similarities.

Further collecting from the same bed has yielded quite numerous pollen-bearing cones. Among these were the two new specimens of *C. comptonensis* from which Taylor and Alvin (1984) obtained pollen for their study of wall development in *Classopollis*. The same study, however, indicated that a different type of male cone was also present, evidenced by its different pollen; it was attributable to the pollen genus *Araucariacites* Cookson *ex* Couper (Batten, pers. comm.). Indeed, it has now become clear that the great majority of the cones retrieved from the bed belong to this other species. Of some thirty cones which have been recovered, only three complete, and a few fragments can be identified as *C. comptonensis*. Moreover, examination of the original material on which this species was erected has shown that it was also mixed. It is therefore necessary to emend *C. comptonensis* and describe the other cone as a new species of *Masculostrobus* Seward, a form-genus of coniferous pollen cones not attributable to any family. In the course of our study, some new information has emerged concerning the structure of the microsporophyll of *C. comptonensis*. In the light of this, we discuss the possible significance of some of the unusual features of the cheirolepidiaceous male cone.

MATERIALS AND METHODS

Most of the specimens have been obtained by bulk breakdown of dried blocks of matrix. The blocks were soaked in water for several hours after which the material was sieved, washed and, with the material left in water, searched under a stereoscopic microscope. Cuticles were prepared by using Schulze's macerating fluid, followed by 5 per cent potassium hydroxide and mounted either in glycerine jelly for light microscopy or on stubs using double-sided adhesive tape for scanning electron microscopy. Unmacerated pieces were mounted for SEM in the same way. Material softened overnight in 2 per cent potassium hydroxide dissolved in 70 per cent alcohol was used for dissection. All specimens (numbers prefixed V.) are in the Palaeontology Collections, Natural History Museum, London.

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SYSTEMATIC PALAEONTOLOGY

Family CHEIROLEPIDIACEAE Takhtajan, 1963
Form-genus CLASSOSTROBUS Alvin *et al.*, 1978

Type species. Classostrobus comptonensis Alvin *et al.*, 1978

Classostrobus comptonensis Alvin *et al.*

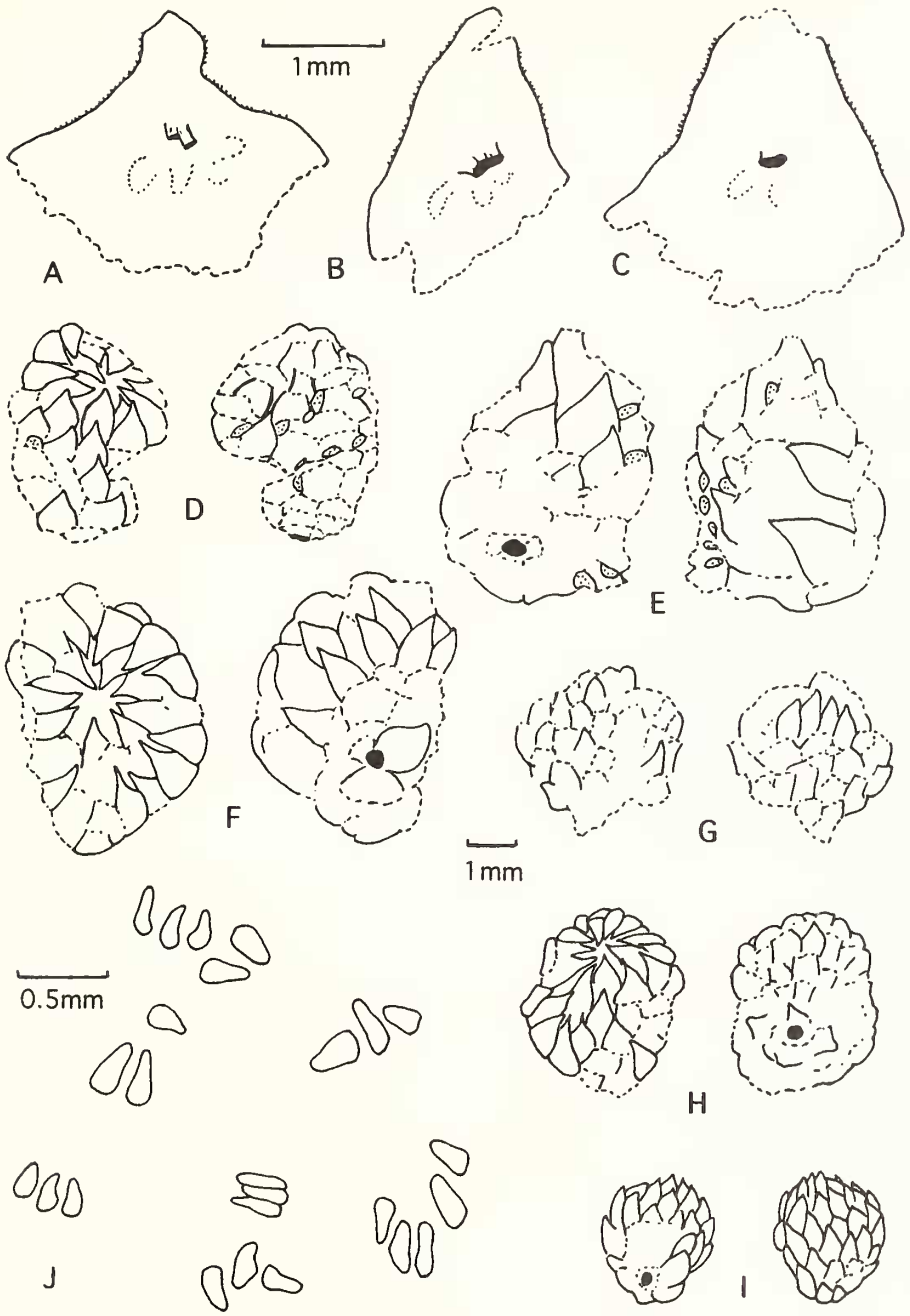
Text-figure 1A–C

Emended diagnosis. Cone spherical to ellipsoidal, with maximum dimensions 14 mm and 12 mm. Microsporophylls spirally arranged, imbricated, peltate, consisting of a laminate head with centrally attached stalk 0·3–0·7 mm in diameter and 1–2 mm long; head rhomboidal, 2–4 mm long, 1·5–3·0 mm wide, with acute apex (56–80°), upper portion (exposed on cone surface) thick with papillate surface and marginal hairs up to 60 μm long; lower portion (covered by heads of lower sporophylls in cone) thinner and more delicate, becoming extremely thin towards lower edge, smooth. Abaxial cuticle of upper portion thick, papillose, with cutinized hypodermis, and stomata in ill-defined rows or more or less scattered; papillae conical, 10–15 μm long, arising singly from epidermal cells; epidermal cells isodiametric, 20–30 μm wide, with anticlinal walls 4–8 μm thick; hypodermal cells isodiametric, 20–30 μm wide or, between stomatal rows, elongated, 10–20 μm wide, stomata sunken, with pit formed by a ring of 5–7 subsidiary cells, each with a papilla up to 15 μm long. Abaxial cuticle of lower portion of sporophyll head thinner, smooth, with stomata confined to upper region; these stomata less sunken and without papillae. Adaxial cuticle of upper portion of sporophyll head thin, papillate in central region down to attachment of stalk, smooth elsewhere; cells isodiametric, not well marked. Sporophyll stalk smooth with elongated epidermal cells 60–80 μm long, 15–30 μm wide. Pollen of *Classopollis*-type, spheroidal with flattened poles, diameter (30–)36(–40) μm × (23–)25(–27) μm [fifteen grains measured], divided into two unequal caps by a subequatorial furrow situated at the distal edge of an equatorial belt (8–)11(–12) μm wide; 9–12 striations in equatorial belt. Pseudopore at distal end 6–11 μm in diameter. Trilete mark at proximal pole with laesurae 5–7 μm long. Exine thickness 1·3 μm; equatorial thickening 2·5 μm. External sculpture fine, of small blunt spines, about 25 elements per μm^2. Internal sculpture vermiculate (see Text-fig. 1A–C).

Types. The holotype is specimen V.59115 (Alvin *et al.* 1978, pl. 97, figs 1–7; pl. 98, figs 1–6; text-fig. 1A); from the Brook Formation (Barremian) between Compton Grange Chine and Hanover Point (OS Grid Ref. SZ 377840), Isle of Wight, southern England.

Description and discussion. The new material on which our revision of this species is based consists of two more or less complete cones (V.63682 and V.63683) and one broken specimen (V.63684).The better preserved cone (V.63682) has allowed a more detailed description of the microsporophyll surfaces and cuticles.

The number of pollen sacs on the microsporophyll, given as three in the original description, was based unfortunately on the small cone illustrated by Alvin *et al.* (1978, pl. 96, figs 8–9; text-fig. 1B–D), a specimen which belongs to the new species described below. The number of pollen sacs in *Classostrobus comptonensis* is therefore unknown. However, on the basis of some evidence from one of the new cones (V.63682), part of which we dissected after softening in alcoholic potash, as well as from some microsporophylls removed from the broken specimen (V.63684), we believe that the number was probably more than two. The dissected cone indicated a very large number of yellowish bodies, presumably remains of pollen sacs, close to the axis, but it was not possible to determine their individuality or how they were associated with the individual microsporphylls. Some microsporophylls removed from the broken cone showed patches of pollen, or small, very indistinct depressions on the lower part of the adaxial side, which suggested that the number might have been



TEXT-FIG. 1. Conifer pollen cones from between Compton Grange Chine and Hanover Point, Isle of Wight, Brook Formation (Barremian). A–C, *Classostrobus comptonensis* Alvin *et al.*; V.63684; isolated microsporophylls showing shallow depressions (indicated by dotted lines) below the stalk, possibly representing attachments of pollen-sacs; lower edge (shown as a broken line) is probably damaged. D–J, *Masculostrobus vectensis* sp. nov. D–I V.63687 to V.63692 respectively; a selection of cones showing the range of size and form; in each, the two sides of the specimen are shown; pollen-sacs are stippled. J, V.63690, typical grouping of pollen-sacs obtained by softening and squashing the cone shown in Text-figure 1G.

three (Text-fig. 1A–C). We envisage that the pollen-sacs were attached to the lower part of the sporophyll and were probably elongated parallel to the stalk. This agrees essentially with Kirchner's (1992) interpretation of the structure of the microsporophyll in *Hirmeriella escheri* (Heer) Kirchner, except that the number of pollen-sacs is about ten per sporophyll in that species.

Family unknown

Form-genus MASCULOSTROBUS Seward, 1911

Type species. Masculostrobus zeilleri Seward, 1911.

Masculostrobus vectensis sp. nov.

Pl. 1, figures 1–7; Text-figure 1D–J

Diagnosis. Cone shortly ellipsoidal to almost spherical (2·2–)3·4(–4·6) mm long, (1·3–)2·7(–3·7) mm wide. Microsporophylls spirally arranged, imbricate, peltate, each consisting of a laminate head and a sub-centrally placed stalk; exposed part of head typically pointed-elongate, *c.* 1·5 mm long, 0·8 mm wide but varying greatly in size more or less proportionally to the size of cone; apex acute (40°–)54°(–75°); scarious border consisting of cells elongated almost at right angles to the edge and becoming a single layer thick with the marginal cells drawn out into free or contiguous hairs. Cuticle of abaxial side thin, showing slightly elongated cell outlines; stomata absent. Pollen sacs borne on lower half of microsporophyll, typically three in number, *c.* 0·4 by 0·15 mm, cylindrical or tapering slightly towards the axis. Pollen of *Araucariacites* type, spherical, inapperturate, (48·0–)57·9(–64·8) μm in diameter [20 grains measured]; exine finely granular with elements *c.* 0·4 μm in diameter and minutely rough surface.

Types. The holotype is specimen V.59117 (Alvin *et al.* 1978, pl. 96, figs 8–9; text-fig. 1C–D); from the Brook Formation (Barremian), between Compton Grange Chine and Hanover Point (O.S. Grid Ref. SZ 377840), Isle of Wight, southern England.

Description and discussion. The quite numerous specimens of this new species present a considerable range, not only in cone and sporophyll size, but also in the plane of compression (Pl. 1, fig. 1; Text-fig. 1D–I). This last variation no doubt relates to the originally almost spherical form. Although the great majority of specimens appear to be fully mature, a few are considerably smaller than average in size and have smaller, more tightly adpressed sporophylls in which the scarious margin is less conspicuous (e.g. Text-fig. 1G, I). Pollen has been obtained in greatly varying quantity from several specimens. In some cones, particularly the smaller ones with closely adpressed microsporophylls, there was a strong tendency for the pollen to adhere together in masses apparently representing portions of pollen-sacs. Sometimes these pollen masses are accompanied by remains of a bounding membrane and usually abundant Ubisch bodies (orbicules). We interpret these specimens as being immature and envisage that maturation was accompanied by expansion of individual microsporophylls. This conforms with what happens typically in most living conifers.

EXPLANATION OF PLATE 1

Figs 1–7. *Masulostrobus vectensis* sp. nov. Between Compton Grange Chine and Hanover Point, Isle of Wight; Brook Formation, (Barremian). 1, V.63685; cone; ×18. 2–4, V.63686, tip of microsporophyll showing extreme apex and fimbriate margin; ×100. 3, detail of marginal hairs; ×650. 4, SEM view of head of microsporophyll with damaged margin and tip, showing epidermal cells; ×120. 5–7, V.63687; views of pollen grain from cone shown in Text-figure 1E. 5, SEM view; ×1250. 6, SEM view of surface; ×10000. 7, light microscope view; ×750.

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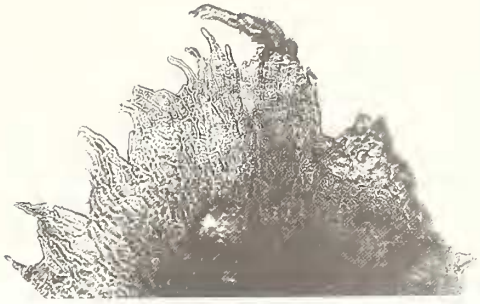

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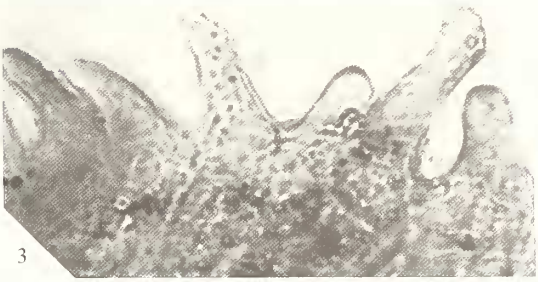

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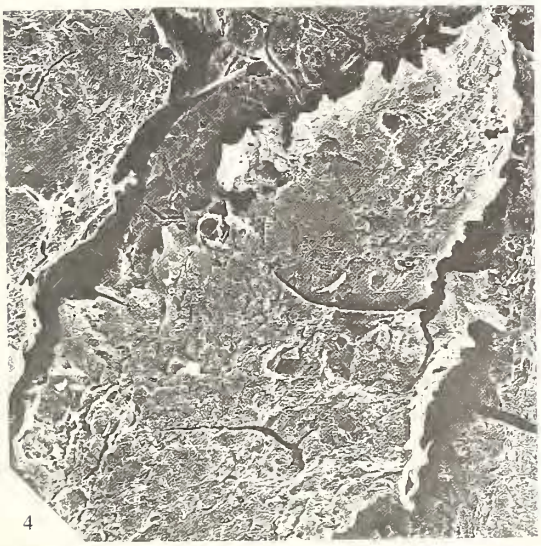

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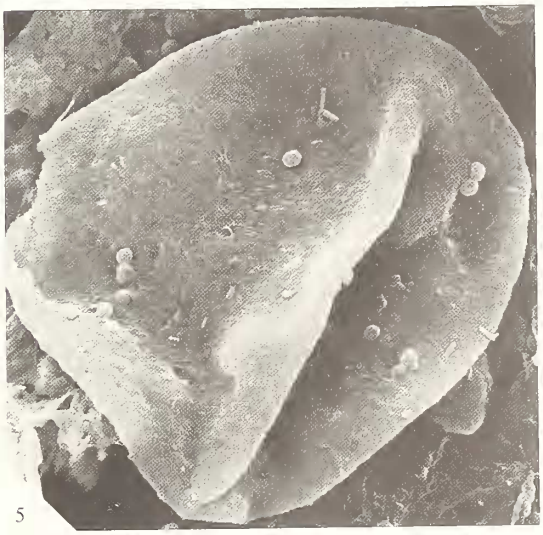

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ALVIN *et al.*, *Masculostrobus*

The specimen shown in Text-figure 1G was judged to represent a young cone. After being softened in alcoholic potash, portions were squashed on a microscope slide and yielded numerous whole pollen sacs; these showed a strongly grouped arrangement (most commonly in threes). This probably reflects the number of pollen sacs on individual microsporophylls (Text-fig. 1J) and thus agrees with the observations originally made on the cone that we now designate as the type specimen (Alvin *et al.* 1978, text-fig. 1C–D).

The sporophyll margin is a distinctive feature, though this is much less conspicuous in the small, probably unexpanded cones, and also in the small sporophylls close to the apex and the base of larger specimens. In unmacerated sporophylls the marginal band becomes translucent as it thins to a single layer of elongated cells at the edge, which are then extended into fringe-like hairs (Pl. 1, figs 2–3). In many examples the sporophyll edge appears smooth and slightly wavy, but this is believed to be due to the breaking off of the hairs; similarly, the extreme tip is usually broken off (Pl. 1, fig. 4).

Cuticles are thin and difficult to prepare, but the abaxial surface of the cleaned but unmacerated sporophyll viewed directly by SEM sometimes shows slightly elongated, bulging epidermal cells (Pl. 1, fig. 4).

Typical pollen grains are shown in Plate 1, figures 5 and 7, and the exine sculpture in Plate 1, figure 6. The pollen characters given in the diagnosis are based mainly on samples obtained from the type specimen and two others (V.63688 and V.63689; Text-fig. 1E–F). The grains from the former had a slightly larger average size than those from the other, though the size ranges overlapped and the maximum size was the same in both. The cone with the slightly larger average size also had a higher proportion of free grains, probably suggesting it was more mature. The degree of roughness of the exine granules is somewhat variable. Although there is no clear evidence of an aperture, squashed or otherwise damaged grains sometimes indicate that there may have been a slightly thinner area of wall.

The structure of *Masculostrobus vectensis* does not itself give any clear indication of family affinity; hence we classify it in this form-genus which was erected by Seward (1911) for male cones of unknown affinity. Cones of the same basic structure are found in a number of extant conifer families. However, the spiral arrangement of the sporophylls, the presence of more than two pollen sacs on the sporophyll and non-saccate pollen represent a combination of features which seems to us more reminiscent of Taxodiaceae or Araucariaceae than of other families. However, the delicate cone structure makes it dissimilar to most living Araucariaceae.

Although remains of plants other than *Pseudofrenelopsis parceramosa* are rare in the deposit and represented only by fragments, leaves and leafy shoots of some three or possibly four other confers are present. These are under investigation.

DISCUSSION

Pseudofrenelopsis parceramosa, represented by ultimate shoots, woody twigs and wood, is often very well preserved and abundant in the same bed which has yielded both of the cones described above (Alvin *et al.* 1981; Alvin 1983). Other plants, in contrast, are infrequent, fragmentary and often not well preserved. It is surprising therefore that specimens of *Classostrobus comptonensis*, attributable on good evidence to *Pseudofrenelopsis parceramosa*, are found only rarely, compared with *Masculostrobus vectensis*. It is even more surprising in view of the comparatively robust structure of the former and the delicate nature of the latter. We tentatively suggest that this may relate to differences in the biology of the two species with regard to pollen shedding and perhaps pollination.

The parent tree of *Masculostrobus vectensisis* is likely to have produced pollen in numerous, short-lived cones, which expanded late in their development and were then shed. Such a scenario is usual in living conifers and indeed in many other wind-pollinated plants. *Classostrobus comptonensis*, like most of the fifteen or so cheirolepidiaceous male cones which have been described (Watson 1988), is unusual in being comparatively robust in structure with the microsporophyll as

thickly cutinized on the exposed abaxial side as the leaf or photosynthetic stem of the same plant. Thick cutinization of the microsporophyll is unusual amongst living conifers. *Araucaria araucana*, which has large, fairly long-lasting male cones, has strong cutinization of the microsporophyll, but the thicker abaxial cuticle is only about half as thick as the leaf cuticle. Whilst the unusual thickness of the microsporophyll cuticle in a cheirolepidiaceous species may be merely part of the generally xeromorphic character of the whole plant, it suggests that the male cone may have been long-lasting rather than ephemeral and, if so, may have shed pollen slowly or perhaps only at intervals over a long period. The fact that all but two or three of the known cheirolepidiaceous male cones have been found in attachment to shoots seems to support this hypothesis. Amongst other fossil conifers attachment is encountered less frequently, presumably because, as in living conifers, the short-lived cones were shed rapidly after pollen dispersal. Is it possible, therefore, that there may have been a mechanism for slow or controlled pollen release in Cheirolepidiaceae? The cone structure gives little clue, but it is noteworthy that in *Classostrobus comptonensis* considerable quantities of pollen are found adhering to the overlapping surfaces of the microsporophylls. Such pollen could conceivably have been released slowly from between these hairy surfaces by small movements of the microsporophylls, made perhaps in response to small changes in atmospheric humidity in much the same way as in the seed-cone scales in living Pinaceae. Many examples of controlled release of disseminules are known among living plants such as the xerochasic release of spores from many moss capsules (Ingold 1965) and the hydrochasic mechanism releasing seeds in some desert plants (Van der Pijl 1969).

Recently, on the basis of their new study of *Hirmeriella muensteri*, Clement-Westerhof and Van Konijnenburg-Van Cittert (1991) have suggested that the pollen might have alighted and germinated on the female cone-scale and that the pollen tubes then grew towards the ovules. This behaviour is well known in a number of present-day conifers (Doyle 1945) but is not correlated with any obvious modification of the male cone, although it is associated in Pinaceae (*Tsuga*) and Podocarpaceae (*Saxegothaea*) with loss of pollen sacci.

The extraordinary elaborate pollen wall structure in *Classopollis* and other circumpolles, recently reviewed by Pocock *et al.* (1990), has led these authors to suggest that the group might have advanced towards entomophily in the Jurassic and Cretaceous. Nevertheless they see some of the wall features as being more especially concerned with permitting volume changes in the grain during transit through the arid environment. If, as we suggest, the pollen remained viable in the mature male cone for a long period after its initial release from the pollen sacs until, perhaps only under certain conditions, being transported by the pollination vector, resistance to desiccation and longevity could have been features of special importance.

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